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ORIGINAL ARTICLE

Evolution of Defence Portfolios in Exploiter–Victim Systems

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Abstract Some organisms maintain a battery of defensive strategies against their exploiters (predators, parasites or parasitoids), while others fail to employ a defence that seems obvious. In this paper, we shall investigate the circumstances under which defence strategies might be expected to evolve. Brood parasites and their hosts provide our main motivation, and we shall discuss why the reed warbler *Acrocephalus scirpaceus* has evolved an egg-rejection but not a chick-rejection strategy as a defence against the common (Eurasian) cuckoo *Cuculus canorus*, while the superb fairy-wren *Malurus cyaneus* has evolved a chick-rejection but not an egg-rejection strategy as a defence against Horsfield's bronze-cuckoo *Chrysococcyx basalis*. We suggest that the answers lie in strategy-blocking, where one strategy (the blocking strategy) prevents the appearance of another (the blocked strategy) that would be adaptive in its absence. This may be common in exploiter–victim systems.

Keywords Evolutionary ecology · Host-parasite systems · Brood parasites · Defence strategies · Rare-enemy effect

1. Introduction

1.1. General introduction

Some organisms employ multiple defence strategies against their exploiters. Bacteria produce many restriction enzymes that attack the genetic material of the bacteriophage species that parasitise them (Levin and Lenski, 1983). The vertebrate immune system is a multi-faceted defence employing many cell types (Roitt and Delves, 2001; Holmes, 1983). Plants tend to synthesise many toxic chemicals as a defence against herbivores (Emlen, 1984, pp. 461–462). Fifty years ago, flax

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Linum usitatissimum was discovered to have 26 genes conferring resistance to a fungal pathogen, the rust *Melampsora lini* (Flor, 1955, 1956). On the other hand, there are cases in which a defence strategy that does not seem evolutionarily unattainable is nevertheless not employed. In our focal example, reed warblers may reject common cuckoo eggs but do not reject their chicks (Davies, 2000). Central American legumes defending themselves against the bruchid beetles that eat their seeds do so by producing either small numbers of poisonous seeds or such large numbers of innocuous seeds that the beetles cannot possibly consume them all, depending on the species, but none makes use of both strategies by producing large numbers of poisonous seeds (Janzen, 1969). In a controversial study, Smith (1968) has suggested that some hosts (oropendolas and caciques) benefit from brood parasitism by cowbirds because the cowbird chicks remove botfly larvae from the host chicks. As a defence against the botfly, the hosts either tolerate cowbirds or nest near wasps or stingless bees (which provide some protection against the flies), but not both (Smith, 1979). Swollen-thorn acacias (*Acacia* spp.) in Central America have evolved a mutualistic relationship with *Pseudomyrmex* ants (Janzen, 1966). The acacias provide the ants with food and shelter, while the ants defend the acacias from herbivores. Other species of acacia synthesise toxic cyanogenic glycosides, which confer protection at least against mammalian herbivores, but none employs both these defence strategies (Rehr et al., 1973).

It is often easy to see why multiple strategies have evolved. First, they may be an adaptive feature of a defence against multiple enemies. The suite of bacterial restriction enzymes and the vertebrate immune system have presumably evolved as such a general defence, the enemies in the case of vertebrate immunity including mutant somatic cells (Marchalonis, 1977). The same is to an extent true of the toxins produced by plants as a defence against herbivores, which are in the vast majority of cases broad-spectrum adaptations to a large suite of enemies (Futuyma, 1983). It is an open question why a complex immune system has not evolved in invertebrates (Marchalonis, 1977), which generally handle invading organisms by phagocytosis and encapsulation (Salt, 1970). The effect of multiple enemies has been reviewed by Sih et al. (1998), and we shall not consider this further. Second, multiple defence strategies may be the result of a coevolutionary arms race (Dawkins and Krebs, 1979). In the paper that brought the word coevolution into general use, Ehrlich and Raven (1964) suggested that toxic compounds developed by plants as a general defence against herbivores provide competition-free resources for herbivores (in this case butterflies) that overcome those defensive barriers. The plant may then produce a further toxin as a defence against the tolerant butterfly (Gilbert, 1971). Certainly, the number of toxins produced by plants seems to increase with the local density of butterflies (Levin, 1976). Alternatively, once the number of tolerant species becomes small, the plant may use a more specialised strategy to defend against them. *Heliconius* butterflies at the larval stage are specialist consumers of passion-vines (*Passifloraceae*), which have evolved two specialised defences against them. They produce hooked hairs that immobilise newly hatched larvae, and structures that mimic *Heliconius* eggs, since *Heliconius* butterflies tend to avoid laying eggs on plants that already have eggs laid on them (Gilbert, 1983). Similar arms races may be seen in plant–pathogen systems. The gene-for-gene relationship discovered in the flax–rust

system by Flor (1956), where each of the 26 rust-resistance genes in the flax has a counteracting virulence gene in the rust, is a striking example. Gene-for-gene relationships have been found in other plant–pathogen systems, mostly involving crop plants (Silvertown and Doust, 1993), and are also seen in plant–herbivore systems, such as the interaction between resistance genes in wheat and virulence genes in the hessian fly *Mayetiola destructor* (Hatchett and Gallun, 1970; Gallun, 1977).

It may be more difficult to see why in some cases the coevolutionary arms race has not taken place. Reed warblers have evolved to recognise common cuckoo eggs, cuckoos have evolved to mimic reed warbler eggs, but reed warblers have not subsequently evolved to recognise cuckoo chicks. In this and the other examples mentioned above, the defence strategy that is employed is certainly imperfect and it seems clear that to employ a further strategy would improve defensive success, yet that strategy has not evolved. There do not seem to be evolutionary constraints that prevent the second defence strategy from evolving, although of course it could be that there has been insufficient evolutionary time for it to do so. In this paper, we shall investigate alternatives to this evolutionary lag hypothesis.

1.2. Rare-enemy effect and strategy-blocking

One of the crucial ideas in this paper is the rare-enemy effect, introduced by Dawkins (1982). He argued that because there are costs involved in any adaptation, it is not advantageous to develop a defence against a rare enemy. In the case of the reed warbler and the common cuckoo the enemy is not particularly rare, with brood parasitism rates often exceeding 20%. However, we shall show that when there are two possible defence strategies that may be deployed against the parasite, each of which is advantageous on its own, an extension of the rare-enemy effect may be used to understand when a combination of the two is advantageous. One strategy may prevent the appearance of the other, a phenomenon we shall call *strategy-blocking*. Let us define a *resource trade-off* between two defence strategies to occur when the employment of one strategy affects the resources available for employing the other, for example if there were a fixed defence budget to be divided between two strategies in the optimal way. A resource trade-off in defence against two enemies is considered by Pointrineau et al. (2003). Such a trade-off increases the probability of strategy-blocking, but we shall show that it is not necessary for strategy-blocking to occur, and shall not include it in our models.

1.3. Brood parasite natural history

The Eurasian cuckoo *Cuculus canorus* is a brood parasite, laying its eggs in the nest of a host species. Typical hosts in Europe are reed warblers, great reed warblers, dunnocks, meadow pipits, robins, and pied wagtails. The female cuckoo visits the host nest during the host's laying period, picks out a host egg, lays her own in its place, and flies off with and eats the host egg. The whole visit lasts about 10 s. Most cuckoo hosts (although not the dunnock) reject eggs that look unlike their own, for example by ejecting them from the nest, and as a consequence the cuckoo egg is usually mimetic, similar to its host's in size, colour, and patterning. When the

cuckoo chick hatches, it balances the host eggs or chicks on its back and pushes them out of the nest. The adult hosts do nothing to prevent this happening, and show very little or no chick-rejection behaviour, although a recent report suggests some rejection by desertion (Grim et al., 2003). On average, in the UK about 5% of reed warbler nests are parasitised, although locally the parasitism rate can rise to over 20%; other species with local parasitism rates of over 40% have been observed (Davies, 2000).

Horsfield's bronze-cuckoo *Chrysococcyx basalis* is an Australian brood-parasite with similar behaviour to the common cuckoo's as adult and chick. A typical host is the superb fairy-wren *Malurus cyaneus*. This host very rarely rejects parasitic bronze-cuckoo eggs, unless they are laid before its own laying period has begun or after it has finished. On the other hand, chick rejection does occur, by desertion of broods containing a single chick (Langmore et al., 2003). Effective parasitism rates in this study ranged from 16 to 32%.

Lotem (1993) explained the lack of chick rejection by the hosts of the common cuckoo as follows. There is some evidence that hosts must learn to recognise their own eggs, by imprinting on their first clutch. There is a problem if this clutch is parasitised, as they would also learn the parasite egg as their own, but at least future unparasitised attempts could be successful. If hosts had to learn to recognise their own chicks, parasitisation of the first clutch by a parasite that ejects host young would be disastrous, as the hosts would not recognise their own chicks and would forfeit all future reproductive success. Some brood parasites do not eject host young, and this argument does not hold; until recently such cases were the only ones where chick rejection had been observed. Examples (Davies, 2000) are a score of species of African finches (paradise whydahs, waxbill whydahs and indigobirds) that parasitise closely related grassfinches, and screaming cowbirds *Molothrus rufoaxillaris* that parasitise bay-winged cowbirds *Molothrus badius*. However, the recent discovery of chick rejection by hosts of ejecting parasites (Langmore et al., 2003) has cast doubt on the universality of Lotem's argument. It does not explain why cuckoo chick rejection has not evolved as an innate trait, and (Langmore et al., 2003) failed to find any evidence that chick-rejecting superb fairy-wrens ever mistakenly imprint on their brood parasites.

A comprehensive review of brood-parasite natural history may be found in Davies (2000).

1.4. Previous models for rejection by brood parasites

Many previous models for egg-rejection have focused either on population dynamics (May and Robinson, 1985) or on population genetics (Rothstein, 1975; Kelly, 1987; Brooker et al., 1990). Takasu and his co-workers (Takasu et al., 1993; Takasu, 1998) were the first to include both ecological and evolutionary aspects of the problem. Planqué et al. (2002) modified these models to include chick rejection as well as egg rejection, and made some progress towards understanding why chick rejection is not observed in the common cuckoo and reed warbler system. Their model neglected sexual reproduction, instead assuming that the number of offspring of each defensive type was proportional to the fitness of that type, and we shall do the same. This makes no difference to our analysis except when there is a

population mixed for defensive type, and then only in determining the proportion of each.

2. Parasitoid or brood-parasite model

2.1. Monomorphic populations

The archetypal model for host–parasitoid systems is Nicholson–Bailey (1935),

$$P' = c(1 - f(P))H, \quad H' = RHf(P), \tag{1}$$

where P and H are the parasitoid and host populations in year t, P' and H' those in year $t + 1$, R the basic reproductive ratio of the host population, $f(P)$ the fraction of hosts that escape parasitism, and c the mean number of parasitoids from each parasitised host that survive to breed. In this model, parasitoids always arise from parasitised hosts: defence is not taken into account. Let us assume instead that a fraction $1 - g$ of parasitised hosts successfully defend themselves against parasitism, and that this defence is cost-free. The model becomes

$$P' = cg(1 - f(P))H, \quad H' = RHf(P) + RH(1 - g)(1 - f(P)). \tag{2}$$

where c is now the mean number of parasitoids from each unsuccessfully defended parasitised host that survive to breed.

However, even in the absence of the parasite, a defence strategy may be costly to maintain. For example, it may be costly for a cuckoo host to adopt a strategy of rejecting eggs that look unlike its own, even in the absence of any cuckoos, if recognition errors imply that it sometimes rejects some of its own eggs (Davies, 2000), and it may be costly for an insect to maintain an immune defence against parasitoids even in their absence (Kraaijeveld and Godfray, 1997; Sasaki and Godfray, 1999). Let the *relative pay-off* of the host defence strategy without parasitism be θ, i.e. $R\theta$ is the expected number of offspring per defending host per year in the absence of parasitism and intra-specific competition. Let the relative pay-off of the host defence strategy with parasitism be φ, i.e. $R\varphi$ is the number of offspring that each parasitised defending host is expected to produce per year in the absence of intra-specific competition. If a host is parasitised, the parasite attack is successful with probability g, which we shall call the *attack success probability*. Host defence is successful with probability $1 - g$, and in this case host offspring are produced. Then the expected number of host offspring conditional on successful defence is $R\varphi/(1 - g)$, in the absence of intra-specific competition. We would expect this to be no greater than the expected number $R\theta$ of offspring produced in the absence of parasitism, and we shall write

$$\varphi = (1 - g)\theta\psi, \quad \text{with} \quad \psi \leq 1. \tag{3}$$

We shall refer to ψ as a *relative pay-off factor*. If successful defence is not costly then we have $\psi = 1$, $\varphi = (1 - g)\theta$, but of course a host may be weakened by

an attack even if its defence is finally successful, in which case we have $\psi < 1$, $\varphi < (1-g)\theta$. In either case, the unconditional expected number of offspring of a parasitised host is $R\varphi < R\theta$. The system becomes

$$P' = cg(1-f(P))H, \quad H' = RH\theta f(P) + RH\varphi(1-f(P)). \tag{4}$$

We shall modify this model to allow survival between seasons and to include self-limitation of the host. We obtain

$$P' = (1-\mu)P + cg(1-f(P))H, \quad H' = \Psi(H;k)Hw(P), \tag{5}$$

where the *relative fitness function* w is given by

$$w(P) = 1 - \nu + R\theta f(P) + R\varphi(1-f(P)). \tag{6}$$

Here μ and ν are the annual probabilities of death for the parasites and the hosts, and R the host annual basic reproductive ratio. An important combination of parameters is the host (lifetime) basic reproductive ratio $R_0 = R/\nu$, the expected number of offspring per host over a lifetime in the absence of parasitism, intraspecific competition and defence costs. With defence costs, this basic reproductive ratio is reduced to $R_0\theta$. The function Ψ in (5) is a self-limitation function such as

$$\Psi(H;k) = \frac{1}{1+H/k}, \tag{7}$$

which models contest competition limiting the host population size in the absence of parasites or defence to a carrying capacity $K = k(R-\nu) = k\nu(R_0-1)$ (Skellam, 1951). Hence k is a scaled version of the host carrying capacity, and will be used later as a bifurcation parameter; however, we shall usually write $\Psi(H)$, suppressing explicit mention of the dependence of Ψ on k. More general functions Ψ satisfying the conditions in the Appendix may also be used.

2.2. Dimorphic populations

Finally, we shall modify the model to allow two host types H_i and H_j. Let $f_i(P)$ (or $f_j(P)$) be the probability that a host of type i (or j) is not parasitised when the parasite population is P; for simplicity we shall take $f_i(P) = f_j(P) = f(P) = \exp(-aP)$, although in some cases different host defence strategies could result in different parasite searching efficiencies a. More general functions f may also be considered, as long as f is a decreasing convex function,

$$f'(P) < 0, \quad 1 - f(P) + Pf'(P) > 0, \tag{8}$$

satisfying $f(0) = 1$ and $f(P) \to 0$ as $P \to \infty$. A straightforward generalisation of (5) gives

$$\begin{aligned} P' &= (1-\mu)P + c_i g_i (1 - f(P)) H_i + c_j g_j (1 - f(P)) H_j, \\ H_i' &= \Psi(H) H_i w_i(P), \quad H_j' = \Psi(H) H_j w_j(P), \end{aligned} \tag{9}$$

where $H = H_i + H_j$ and the *relative fitness function* w_i is given by

$$w_i(P) = 1 - \nu + R\theta_i f(P) + R\varphi_i (1 - f(P)), \tag{10}$$

and similarly for w_j. We have made the simplifying assumption that the two host types are ecologically identical from the point of view of their competitive abilities and requirements, so that the self-limitation depends only on the total host population $H = H_i + H_j$. With the cuckoo example in mind, we have assumed that the costs of the defence strategy impact on fecundity alone, reducing it from R to $R\theta_i$ for type i, where $0 < \theta_i \leq 1$, and similarly for type j, but an increase in the mortality ν gives qualitatively the same results.

In the absence of the parasite, the model becomes

$$H_i' = (1 - \nu + R\theta_i) H_i \Psi(H), \quad H_j' = (1 - \nu + R\theta_j) H_j \Psi(H).$$

Dividing one equation by the other,

$$\left(\frac{H_i}{H_j} \right)' = \frac{1 - \nu + R\theta_i}{1 - \nu + R\theta_j} \frac{H_i}{H_j},$$

so that coexistence is only possible if $\theta_i = \theta_j$: otherwise, the type with the higher value of θ will drive the other type to extinction from any initial conditions. This is a straightforward application of the principle of competitive exclusion, which implies that a population employing one strategy tends to exclude one employing another. The extension to more than two host types is clear; the type with the least costly defence strategy (in the absence of the parasite) prevails. The best strategy of all in this situation, of course, is to refrain from costly defence altogether. We shall refer to this naive strategy as $i = 0$, so that $\theta_0 = 1$.

3. Analysis

The analysis consists of a determination of the bifurcations that occur as k, the scaled host carrying capacity, increases. The bifurcation diagram is shown in Fig. 1(b). On a first reading, it may be helpful to skip to the next section where the conclusions are summarised.

3.1. Single-host type

Let us first consider the case of a single-host type i, so that the model becomes

$$P' = (1-\mu)P + cg\,(1-f(P))\,H_i,$$
$$H_i' = \Psi(H_i)H_i w_i(P) = \Psi(H_i)H_i\,(1-\nu+R\theta_i\,f(P)+R\varphi_i(1-f(P)))\,.$$

The basic reproductive ratio for host i is $R_0\theta_i = R\theta_i/\nu = R_i$, say. As long as $R_i > 1$, $R\theta_i > \nu$, failing which host type i goes extinct under any circumstances and which we shall assume from now on, there is a host-only steady state $(0, H_i^0)$, where H_i^0 is the unique solution of $\Psi(H_i^0;k)(1-\nu+R\theta_i) = 1$, and is an increasing function of k since $\frac{\partial H}{\partial k} = -\frac{\partial \Psi}{\partial k}/\frac{\mathrm{d}\Psi}{\mathrm{d}H}$. (For $\Psi(H) = 1/(1+H/k)$, $H_i^0 = k(R\theta_i-\nu) = k\nu(R_i-1)$.) It is stable to perturbations in the (P, H_i) plane for k small, and loses stability to a coexistence state (P_i^*, H_i^*) via a transcritical bifurcation at $k = k_{ip}$. At the bifurcation point $P_i^* = 0$, $H_i^* = H_i^0 = \mu/(cg_i|f'(0)|)$, and k_{ip} is the unique solution of $\Psi(H_i^*;k_{ip})(1-\nu+R\theta_i) = 1$. (For $\Psi(H) = 1/(1+H/k)$, $k_{ip} = \mu/(cg_i(R\theta_i-\nu)|f'(0)|)$.) As we showed in Section 2.2, the only host-only steady state $(0, H_i^0)$ stable to the addition of any of the other host types is that with $i = 0$. Hence, the bifurcation point $k = k_{0p}$ plays a special role, and we shall write $k_{0p} = k_p$.

3.2. Coexistence of the parasite with a single-host type

The coexistence state (P_i^*, H_i^*) with $P_i^* > 0$ for $k > k_{ip}$ satisfies

$$\mu P = cg(1-f(P))H, \tag{11}$$
$$(\Psi(H))^{-1} = w(P) = 1-\nu+R\theta f(P)+R\varphi(1-f(P)), \tag{12}$$

where we have dropped the asterisks and the subscripts. It is straightforward (although somewhat long-winded, see Appendix) to show that P_i^* and H_i^* are both increasing functions of k. Equation (11) is satisfied when $P = 0$ (giving the host-only steady state $(0, H_i^0)$), or when (P, H) lies on the curve

$$H = \frac{\mu}{cg}\frac{P}{1-f(P)}.$$

On this curve,

$$\frac{\mathrm{d}H}{\mathrm{d}P} = \frac{\mu}{cg}\frac{1-f(P)+Pf'(P)}{(1-f(P))^2}.$$

If f is convex then $1-f(P)+Pf'(P) > 0$, and the non-trivial branch of (11) defines H as an increasing function of P. On the other hand, Eq. (12) defines H as a decreasing function of P; the curves cross in the positive quadrant, and the coexistence state is unique, if $k > k_{ip}$. Its stability is determined by the eigenvalues of

the Jacobian matrix $\hat{J}$ at the steady state given by

$$\hat{J} = \hat{J}(P, H) = \begin{pmatrix} \hat{J}_{11} & \hat{J}_{12} \\ \hat{J}_{21} & \hat{J}_{22} \end{pmatrix}$$
$$= \begin{pmatrix} 1 - \mu - cgf'(P)H & cg(1 - f(P)) \\ \Psi(H)HR(\theta - \varphi)f'(P) & (\Psi'(H)H + \Psi(H))w(P) \end{pmatrix}. \tag{13}$$

Now

$$\begin{aligned} \mathrm{tr}\hat{J} &= 1 - \mu - cgf'(P) + (\Psi'(H)H + \Psi(H))w(P), \\ \det \hat{J} &= (1 - \mu - cgf'(P)H)(\Psi'(H)H + \Psi(H))w(P) \\ &\quad - cg(1 - f(P))\Psi(H)HR(\theta - \varphi)f'(P). \end{aligned}$$

Clearly $\mathrm{tr}\hat{J} > 0$ by (8) and (A.1), so the Jury conditions for stability are $\mathrm{tr}\hat{J} < \det \hat{J} + 1$, $\det \hat{J} < 1$. We have

$$\begin{aligned} 1 + \det \hat{J} - \mathrm{tr}\hat{J} &= 1 + (1 - \mu - cgf'(P)H)(\Psi'(H)H + \Psi(H))w(P) \\ &\quad - cg(1 - f(P))\Psi(H)HR(\theta - \varphi)f'(P) \\ &\quad - 1 + \mu + cgf'(P) - (\Psi'(H)H + \Psi(H))w(P) \\ &= -\mu\Psi'(H)Hw(P) \\ &\quad - cgf'(P)(\Psi'(H)H + \Psi(H))w(P) \\ &\quad - cgf'(P)\Psi(H)R(\theta - \varphi)(1 - f(P)) > 0, \end{aligned}$$

where we have several times made use of the fact that $\Psi(H)w(P) = 1$. However, it is not necessarily true that $\det \hat{J} < 1$. In particular, if $\mu = \nu = 1$, $\Psi(H) = 1$, $\theta = 1$, $g = 1$, the model reduces to that of (Nicholson and Bailey, 1935), which is unstable to growing oscillations, and $\det \hat{J} = R\log R/(R-1) > 1$ for $R > 1$. A value of ν less than 1 or a limiting function $\Psi(H)$ both have a tendency to stabilise the steady state. In particular, the steady state is stable for typical values of the parameters in the literature for the cuckoo system (Cramp, 1988; Cramp and Brooks, 1992). Henceforth, we shall assume that the system does not exhibit a Naimark–Sacker bifurcation (often referred to as a Hopf bifurcation for difference equations) for relevant parameter values, so that oscillatory solutions do not occur. Naimark–Sacker bifurcations were considered in Planqué et al. (2002).

3.3. Invasion of a second host type

Now, let us consider the possibility that host type j can invade the steady state of a parasite coexisting with host type i. We assume that the (P, H_i) subsystem has a stable coexistence steady state (P_i^*, H_i^*). In particular, this implies that

$$\Psi(H_i^*)w_i(P_i^*) = 1. \tag{14}$$

Then, the full system has a steady state at $(P_i^*, H_i^*, 0)$. Its stability is determined by the eigenvalues of the Jacobian matrix given by

$$J(P_i^*, H_i^*, 0) = \begin{pmatrix} \hat{J}_{11}(P_i^*, H_i^*) & \hat{J}_{12}(P_i^*, H_i^*) & cg_j(1 - f(P_i^*)) \\ \hat{J}_{21}(P_i^*, H_i^*) & \hat{J}_{22}(P_i^*, H_i^*) & \Psi'(H_i^*)H_i^* w_i^* \\ 0 & 0 & \Psi(H_i^*)w_j^* \end{pmatrix},$$

where $w_i^* = w_i(P_i^*)$, $w_j^* = w_j(P_i^*)$, and $\hat{J}$ is as in Eq. (13). The eigenvalues are those of the Jacobian matrix $\hat{J}$ at the steady state of the (P, H_i) subsystem, assumed stable, and the invasion eigenvalue

$$\lambda = \Psi(H_i^*)w_j(P_i^*) = \Psi(H_i^*)\left(1 - \nu + R\theta_j f(P_i^*) + R\varphi_j(1 - f(P_i^*))\right).$$

Hence, the type-i steady state can be invaded by type j if $\lambda > 1$,

$$\Psi(H_i^*)w_j(P_i^*) > 1. \tag{15}$$

Comparing this with Eq. (14), this is simply the condition that type j be fitter than type i at the steady state, $w_j(P_i^*) > w_i(P_i^*)$.

Similarly, a type-j steady state $(P_j^*, 0, H_j^*)$, with

$$\Psi(H_j^*)w_j(P_j^*) = 1, \tag{16}$$

can be invaded by type i if

$$\Psi(H_j^*)w_i(P_j^*) > 1, \tag{17}$$

$w_i(P_j^*) > w_j(P_j^*)$. Note that mutual invasion and hence coexistence is not possible in the absence of competition, when $\Psi(H) = 1$. For then, we must have both $w_j(P_i^*) > w_j(P_j^*)$ and $w_i(P_j^*) > w_i(P_i^*)$, so (since each w is decreasing) both $P_i^* < P_j^*$ and $P_j^* < P_i^*$, a contradiction. This exclusion is what we would expect, of course, since the two types are then in apparent competition with each other (Holt, 1977), limited by a single factor, the parasite.

Let us investigate the possibility that with competition there exists a bifurcation point k_{ij} beyond which type j invades $(P_i^*, H_i^*, 0)$, giving a bifurcating branch $(P^{**}, H_i^{**}, H_j^{**})$ with neither $H_i^{**} = 0$ nor $H_j^{**} = 0$. This does not contradict the principle of competitive exclusion since there are now two limiting factors, the parasite and inter-type competition. Despite this, it seems at first sight that such a branch cannot exist, because at each value of P (except at a finite set where the fitness curves cross) there is a fittest host that must exclude all others. It is this finite set that is the key to the bifurcation, because at any such bifurcation point, $\Psi(H_i^*)w_j(P_i^*) = 1$, so $w_j(P_i^*) = w_i(P_i^*)$, and the two types i and j have equal fitness. This gives

$$1 - \nu + R(\theta_j - \varphi_j)f(P_i^*) + R\varphi_j = 1 - \nu + R(\theta_i - \varphi_i)f(P_i^*) + R\varphi_i,$$

so $P^{**} = P_i^*$ is the solution P, if any, of

$$f(P) = \frac{\varphi_j - \varphi_i}{\theta_i - \theta_j + \varphi_j - \varphi_i}. \tag{18}$$

Let us assume (without loss of generality) that $\theta_i > \theta_j$, i.e. that host type i is fitter than host type j in the absence of parasitism. Then a necessary condition for such a bifurcation is that $\varphi_j > \varphi_i$, i.e. that host type j is fitter than host type i at high-parasite populations P, as might be expected. If this condition and the conditions on f hold, then (18) has a unique solution $P = P_{ij}$, with

$$w_i(P) = w_j(P) = 1 - \nu + R\frac{\theta_i\varphi_j - \theta_j\varphi_i}{\theta_i - \theta_j + \varphi_j - \varphi_i}.$$

Then $H = H_{ij}$ is given by Eq. (11). Moreover (by the conditions on Ψ as a function of k), the equation $\Psi(H;k)w_i(P) = \Psi(H;k)w_j(P) = 1$ can be solved for $k = k_{ij}$ as long as $w_i(P) = w_j(P) > 1$, or

$$R(\theta_i\varphi_j - \theta_j\varphi_i) > \nu(\theta_i - \theta_j + \varphi_j - \varphi_i). \tag{19}$$

3.4. Coexistence of parasite and two host types

In this section, we assume that, of two host types i and j, i has the greater pay-off when unparasitised, $\theta_i > \theta_j$, while j has the greater pay-off when parasitised, $\varphi_j > \varphi_i$. We assume that Eq. (19) holds, so that we can find the potential bifurcation point k_{ij} beyond which type j invades type i, and the values of P and H there, given by P_{ij} and H_{ij}. We now investigate the coexistence steady state (P^{**}, H_i^{**}, H_j^{**}) for $k > k_{ij}$. Construction of this bifurcating branch involves solving the steady-state equations

$$P = (1-\mu)P + cg_i(1 - f(P))H_i + cg_j(1 - f(P))H_j,$$
$$\Psi(H)w_i(P) = 1, \quad \Psi(H)w_j(P) = 1.$$

This can be done near the bifurcation point as long as M is nonsingular, where

$$M = \begin{pmatrix} \mu + cHg_i f'(P) & -cg_i(1 - f(P)) & -cg_j(1 - f(P)) \\ \Psi(H)w_i'(P) & \Psi'(H)w_i(P) & \Psi'(H)w_i(P) \\ \Psi(H)w_j'(P) & \Psi'(H)w_j(P) & \Psi'(H)w_j(P) \end{pmatrix}.$$

But, since $w_i(P) = w_j(P)$, $\det M = \Psi(H)(w_i'(P) - w_j'(P))\Psi'(H)w_i(P)c(g_i - g_j)(1 - f(P)) \neq 0$, M is nonsingular as long as $g_i \neq g_j$, and there is a transcritical bifurcation at $k = k_{ij}$. We have $w_i(P) = w_j(P)$, so that P is constant, equal to its value P_{ij} at the bifurcation point, everywhere on the bifurcating branch. Host types i and j have equal fitness everywhere on the branch, which uniquely determines the parasite population P. We also have $\Psi(H;k)w_i(P) = 1$, so that the value of

$\Psi(H;k)$ remains the same, everywhere on the bifurcating branch. This defines H^{**} as an increasing function of k. (In the case $\Psi(H;k) = 1/(1 + H/k)$, the function is given by $H^{**} = kH_{ij}/k_{ij}$.) It remains to find the proportions of each type of host. Let us define α by $H_i^{**} = (1-\alpha)H^{**}$, $H_j^{**} = \alpha H^{**}$, so that $\alpha = 0$ at the bifurcation point. We have

$$\mu P^{**} = cg_i(1 - f(P^{**}))(1-\alpha)H^{**} + cg_j(1 - f(P^{**}))\alpha H^{**},$$

so that

$$\alpha = \frac{g_i(H^{**} - H_{ij})}{(g_i - g_j)H^{**}}.$$

If $g_i > g_j, \alpha > 0$ and the branch is biologically realistic for $H^{**} > H_{ij}, k > k_{ij}$, while if $g_i < g_j$ it is realistic for $k < k_{ij}$. There is a further transcritical bifurcation at a point k_{ji}, where α becomes equal to 1, H_i becomes extinct and only H_j persists, which can be analysed in exactly the same way. This point is obtained by solving the system $\Psi(H;k) = \Psi(H_{ij};k_{ij})$, $g_j H = g_i H_{ij}$, for $H = H_{ji}$ and $k = k_{ji}$. (In the case $\Psi(H;k) = 1/(1 + H/k)$, $k_{ji} = g_i k_{ij}/g_j$, $H_{ji} = g_i H_{ij}/g_j$.)

3.5. Limiting behaviour as $k \to \infty$

We have seen that the steady-state values $P^*(k)$ and $H^*(k)$ of P and H both increase as k increases. Here, we shall investigate their limiting behaviour as $k \to \infty$. Since each pair of host types can only coexist in a finite k-interval, then as $k \to \infty$ we can restrict attention to a single-host type. Let us assume first that $R\varphi \geq \nu$ for this host type. In this case, we claim that $P^*(k) \to \infty$, $H^*(k) \to \infty$ as $k \to \infty$. For if not they are *both* bounded (by (11)), so $H^*(k) \leq \bar{H}$, $P^*(k) \leq \bar{P}$, for constants $\bar{H}$ and $\bar{P}$ independent of k. Hence (since w is decreasing), $w(P^*(k)) \geq w(\bar{P}) \geq 1 + R(\theta - \varphi)f(\bar{P}) = 1 + \varepsilon$, say. Let $k = \bar{k}$ be the unique solution of $\Psi(\bar{H};k) = (1+\varepsilon)^{-1}$. Then (since Ψ is increasing in H and decreasing in k), $\Psi(H^*(k);k)w(P^*(k)) > 1$ for $k > \bar{k}$, contradicting Eq. (12) and verifying the claim.

The condition $R\varphi \geq \nu$, or $R_0\varphi > 1$, implies that the host type can flourish whatever the parasite population P as long as k is sufficiently large. Let us now assume that $R\varphi < \nu$ for every type. As before, we may restrict attention to a single-host type. Since $P^*(k)$ is an increasing function of k, we know that $P^*(k) \to \infty$ or to a finite limit $\bar{P}$ as $k \to \infty$. First, we claim that $P^*(k)$ tends to a finite limit. For if not, $w(P^*(k)) \to 1 - \nu + R\varphi < 1$ as $P^*(k) \to \infty$. Let $k = \bar{k}$ be the solution of $w(P^*(k)) = 1$. Then $w(P^*(k)) \leq 1$ for $k \geq \bar{k}$, and $\Psi(H^*(k);k) < 1$ for all k, so $\Psi(H^*(k);k)w(P^*(k)) < 1$, contradicting Eq. (12). Second, we claim that $P^*(k) \to P_\infty$ as $k \to \infty$, where P_∞ is the (unique and finite) solution of $w(P) = 1$, (and hence $H^*(k) \to H_\infty$, given by Eq. (11) with $P = P_\infty$). Clearly, it cannot tend to a limit $\bar{P}$ with $w(\bar{P}) < 1$, by the argument above, so assume for contradiction that it tends to a limit with $w(\bar{P}) > 1$. Then $H^*(k) \to \bar{H}$ given by Eq. (11) with $P = \bar{P}$. Let $k = \bar{k}$ be the (unique) solution of $\Psi(\bar{H};k) = 1/w(\bar{P}) < 1$. Then for $k > \bar{k}$, $\Psi(H^*(k);k)w(P^*(k)) > \Psi(\bar{H};\bar{k})w(\bar{P}) = 1$, contradicting Eq. (12).

4. Synthesis: Theoretical results

4.1. First view

Although we have only looked at two host types at a time, it is now easy to see what happens as k increases in any system with any number of host types, unless Naimark–Sacker bifurcations to oscillatory behaviour occur. The crucial features of the system may be seen by plotting the graphs of the relative fitness functions w_i against parasite population P, as shown for two types in Fig. 1(a). The corresponding bifurcation diagram is shown in Fig. 1(b).

As k increases, P increases, and the host type that survives is the fittest for that P, i.e. the one with the highest value of the relative fitness function w. But it is not quite as simple as that. First, P is not strictly increasing with k. So, at first, P remains at 0 until k reaches a bifurcation point $k_p(= k_{0p})$, defined in Section 3.1. In this interval, the host type is the one with the highest value of $w_i(0) = 1 - \nu + R\theta_i$, i.e. the one that does not defend itself against the parasite at all ($i = 0$). Beyond k_p, P starts to increase from zero, but at first the resident host type is still the non-defender, as we would expect as a consequence of the rare-enemy effect (Dawkins, 1982). The next bifurcation occurs at the first crossing of the graph of w_i with another graph w_j, at a bifurcation point k_{ij} defined in Section 3.4. If $g_i > g_j$ (which is certainly true if $i = 0$), then P again stops increasing with k at this point, and remains constant until the next bifurcation point k_{ji} defined in Section 3.4. In the interval (k_{ij}, k_{ji}), the proportion of the host that is of type j rises steadily from 0 to 1. When all the host is of type j, we are back in the single-host case and P starts to increase again. On the other hand, if $g_i < g_j$, host type j immediately replaces host type i beyond k_{ij}, and P continues to increase without a break. In either case, we are back to the case of a single-host type, and the same process of invasion and eventual or immediate fixation of a new type may occur again. The limiting behaviour as $k \to \infty$ depends on whether there exists a host type i with $R\varphi_i > \nu$. If so, then we follow the curve of maximum w to its limit as $P \to \infty$, and

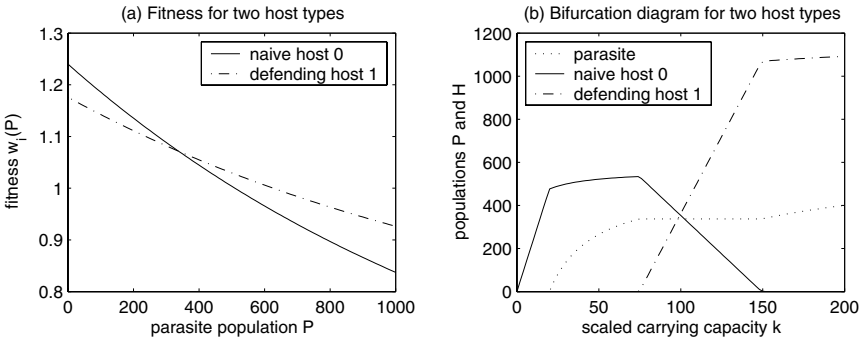

Fig. 1 (a) The fitness functions w_0 and w_1 for a naive and a defending host. (b) The corresponding bifurcation diagram, with bifurcation points given approximately by $k_p(= k_{0p}) = 20$, $k_{01} = 75$, $k_{10} = 150$. The population sizes are in arbitrary units.

we end up on the fitness curve for the type with maximum φ_i, or maximum fitness at high-parasite population P. If not, then we only follow the curve of maximum w towards a limiting point $(P, w) = (P_\infty, 1)$. However much k increases, parasite population P does not increase beyond P_∞, and the limiting host type is the one that crosses $w = 1$ last.

4.2. Second view

An alternative way to present these results is to think of parasitism not in terms of the parasite population P but in terms of the probability $\pi = 1 - f(P)$ of suffering parasitism. We shall refer to π as the *parasitism pressure*. Let $v_i(\pi) = (w_i(f^{-1}(1 - \pi)) - 1)/v$ be the expected excess per capita lifetime production of host type i when the parasitism pressure is π in the absence of intra-specific competition. A positive value of v_i implies that the population of host type i would grow in the absence of competition, and a negative value that it would decay. The fitness curves v_i are now just straight lines in the (π, v) plane, joining the point $(0, R_0\theta_i - 1)$ to the point $(1, R_0\varphi_i - 1)$. Let $\theta_i > \theta_j$ and $\varphi_i < \varphi_j$. Then, the lines for host types i and j cross each other at $(v, \pi) = (v_{ij}, \pi_{ij})$ with $0 < \pi_{ij} < 1$, where

$$\pi_{ij} = \frac{\theta_i - \theta_j}{\theta_i - \theta_j + \varphi_j - \varphi_i}.$$

If i is the fittest strategy of all for π less than and sufficiently close to π_{ij}, then j is the fittest for π greater than and sufficiently close to π_{ij}, and the stable host type moves from i to j as the parasitism pressure moves up through π_{ij}. If $R_0\theta_i > 1 > R_0\varphi_i$, such a line cuts the π axis at $(\pi_i^*, 0)$, where $\pi_i^* = (R_0\theta_i - 1)/(R_0(\theta_i - \varphi_i))$, while if $R_0\theta_i > R_0\varphi_i > 1$ the host can withstand arbitrarily high parasitism pressure, and we define $\pi_i^* = 1$. We shall call π_i^* the *maximum attainable parasitism pressure* for type i, written in terms of the probability of parasitism, although it is in fact only attained in the limit as $k \to \infty$ or if $\Psi(H) = 1$. As k increases, the last host type to remain is the one with the largest value of π_i^*. If more than one host can withstand arbitrarily high parasitism pressure then the survivor is the one with the highest value of φ. This is not surprising: the fact that $k \to \infty$ implies that we are again in a situation of apparent competition (Holt, 1977), where the hosts are limited by a single factor, the parasite. The P^* rule of apparent competition states that when two species that do not compete directly with each other are both limited by the same predator, then the one that can survive the higher predator population P^* will drive the other to extinction. Here, there is a parallel π^* rule: as $k \to \infty$, the host type to survive is the one with the highest maximum attainable parasitism pressure π^*.

5. Optimal defence portfolios

Let us consider now the question of an optimal defence portfolio. If you have two potential defence mechanisms at your disposal (in evolutionary terms), do you employ one of them, both of them, or none at all? If you employ just one, which

one should it be? For example, should a parasitoid host attempt to encapsulate parasitoid eggs, or to mount a phagocytic response against them, or both? Should a cuckoo host attempt to remove cuckoo eggs, or cuckoo chicks, or both? We shall label the single strategies 1 and 2, the combined strategy 3, and the strategy of mounting no defence 0. The optimal portfolio depends on

- the fitness parameters θ_1 and θ_2 relating to the defence strategies 1 and 2 in the absence of the exploiter, and the relationship of θ_3 to them,
- the fitness parameters φ_1 and φ_2 relating to defence strategies 1 and 2 in the presence of the exploiter, and the relationship of φ_3 to them,
- the ecological parameters $R_0 = R/\nu$ and k.

5.1. Strategy-blocking

We introduce the concept of *strategy-blocking*. Recall the definition of $v_i(\pi)$ as the expected excess *per capita* lifetime production of host type i when the parasitism pressure is π, in the absence of intra-specific competition. If $v_i(\pi) > v_j(\pi)$ at a parasitism pressure π, then (unless strategy i does not appear for some reason such as evolutionary lag), strategy j will not be observed at that parasitism pressure. If $v_i(\pi) > v_j(\pi)$ for all $\pi \in (0, 1)$, then strategy j will not be observed whatever the parasitism pressure, and we shall say that strategy i *unconditionally blocks* strategy j. If, for all $\pi \in (0, 1)$, either $v_i(\pi) > v_j(\pi)$ or $v_0(\pi) > v_j(\pi)$, where strategy 0 is the naive strategy, we shall also say that strategy i unconditionally blocks strategy j. If, for all $\pi \in (0, 1)$, either $v_0(\pi) > v_2(\pi)$ or $v_1(\pi) > v_2(\pi)$ *and* either $v_0(\pi) > v_3(\pi)$ or $v_1(\pi) > v_3(\pi)$, where strategy 3 is strategy 1 combined with strategy 2, then we shall say that strategy 2, either on its own or combined in strategy 3, is blocked by strategy 1. We argue that strategy-blocking is the key to understanding why some defence strategies have *not* evolved. This is particularly true in the apparently paradoxical case where (i) $v_2(\pi) > v_0(\pi)$ for some π, but (ii) $v_1(\pi) > v_2(\pi)$ and (iii) either $v_0(\pi) > v_3(\pi)$ or $v_1(\pi) > v_3(\pi)$ for all π. Condition (i) invites the conclusion that strategy 2 can be advantageous, but conditions (ii) and (iii) imply that it cannot persist (on its own or in combination) in competition with strategy 1.

Although π theoretically varies between 0 and 1, true parasitism pressures are determined by ecological parameter values. We define *conditional strategy-blocking* in such cases. For example, if $v_i(\pi) > v_j(\pi)$ for all $\pi \in (\underline{\pi}, \overline{\pi})$, we say that strategy i blocks strategy j conditionally in $(\underline{\pi}, \overline{\pi})$. Figure 2 illustrates conditional strategy-blocking.

5.2. Naive versus defensive strategies

We start by comparing the naive strategy 0 with the defensive strategy 1. The naive strategy has $\theta_0 = 1$ but $\varphi_0 = 0$, while the defensive strategy has $\theta_1 < 1$ and $0 < \varphi_1 = \theta_1\psi_1(1 - g_1)$ with $\psi_1 \leq 1$. If $R_0\varphi_1 > 1$, then the defending host can withstand arbitrarily high parasitism levels, and will drive the naive host to extinction at high values of k. If $R_0\varphi_1 < 1$, then the defending host can withstand a probability

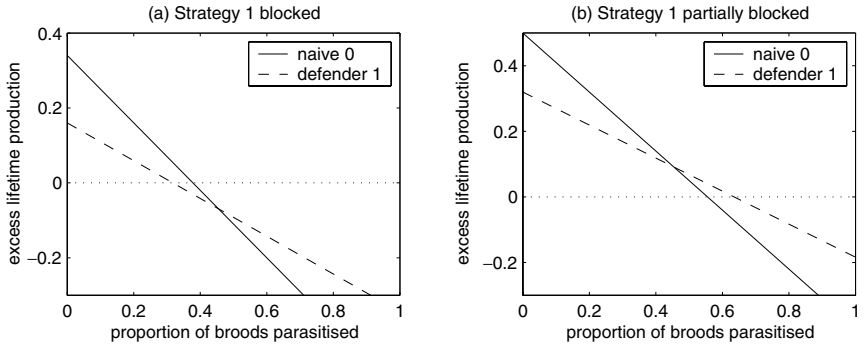

Fig. 2 Conditional strategy-blocking. The naive strategy blocks any defensive strategy if π is small, and may do so for all feasible values of π, as shown in panel (a), even if the defence strategy offers certain success. However, feasible values of π are determined by the ecological parameter values, and the defensive strategy will not be blocked if both k and R_0 are sufficiently high, as shown in panel (b). For a sketch of the corresponding (k, R_0) plane see Fig. 6(b), with say $R_0 = 1.1$ for (a) and $R_0 = 1.4$ for (b).

$\pi_1^* = (R_0\theta_1 - 1)/(R_0(\theta_1 - \varphi_1))$ of parasitism, while the naive host can withstand $\pi_0^* = (R_0 - 1)/R_0$. If $\pi_1^* < \pi_0^*$, then the defending host never invades, while if

$$\pi_1^* = \frac{R_0\theta_1 - 1}{R_0(\theta_1 - \varphi_1)} = \frac{R_0\theta_1 - 1}{R_0\theta_1(1 - \psi_1(1 - g_1))} > \frac{R_0 - 1}{R_0} = \pi_0^*, \tag{20}$$

it invades and drives the naive host to extinction for sufficiently high host carrying capacity. This holds as long as $R_0\theta_1 - 1$ is sufficiently high, i.e. the defending host is fit enough in the absence of parasitism, and $\theta_1 - \varphi_1$ is sufficiently low, i.e. parasitism is not too costly to the defending host. For fixed defence strategy parameters θ_1, ψ_1 and g_1, it holds if R_0 is sufficiently high. For fixed R_0, it holds if ψ_1 is sufficiently close to 1 and g_1 is sufficiently low, i.e. the conditional defence costs are sufficiently small and the success probability of the defence is sufficiently high. Note that even if $g_1 = 0$, so that the defence strategy offers certain success, we still require ψ_1 to be sufficiently close to 1 for it to invade. Otherwise the strategy results in a Pyrrhic victory, defined by the Oxford English Dictionary as 'a victory gained at too great a cost'. In this case, the costs outweigh the benefits of defeating the parasite, and it never invades the naive strategy.

5.3. Single defensive strategies

We now compare the defensive strategies 1 and 2, with $\theta_1 > \theta_2$, assuming as usual that $R_0\theta_1 > 1$, $R_0\theta_2 > 1$. If $\varphi_1 > \varphi_2$ then strategy 1 is always fitter than strategy 2, so a necessary condition for strategy 2 ever to invade is that it must be fitter at high parasitism pressures,

$$\varphi_2 = \theta_2\psi_2(1 - g_2) > \theta_1\psi_1(1 - g_1) = \varphi_1.$$

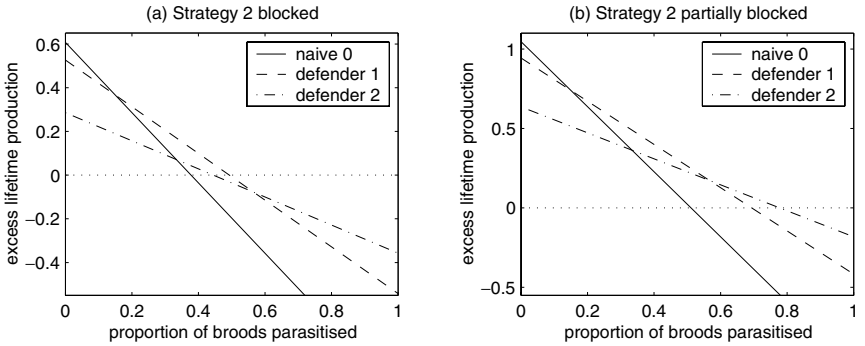

Fig. 3 The naive strategy is always fittest for low parasitism pressures. The defence strategy parameters (θ_i, ψ_i and g_i) are chosen so that strategy 2 is fittest at high parasitism pressure, but strategy 1 is fittest at intermediate values. The figure shows the effect of varying R_0. In panel (a) R_0 is low, and strategy 2 is blocked at any feasible parasitism pressure. In panel (b) R_0 is higher, and high values of k lead to parasitism pressure high enough for strategy 2 to be fittest. (Parameter values $\theta_1 = 0.95$, $\theta_2 = 0.8$, $g_1 = 0$, $g_2 = 0$, $\psi_1 = 0.3$, $\psi_2 = 0.5$, (a) $R_0 = 1.6$, (b) $R_0 = 2.0$.)

Since $\varphi_i = \theta_i \psi_i (1 - g_i)$, the strategy that is worse in the low-parasite environment (strategy 2) can only pay off in a high-parasite environment if its unconditional pay-off θ_2 is not too small, its conditional pay-off factor ψ_2 is not too small, and its success probability $1 - g_2$ is sufficiently high, compared with those of strategy 1. Note that even if $g_2 = 0$, so that defence strategy 2 offers certain success, it offers a Pyrrhic victory and is unconditionally blocked by strategy 1 if $\psi_2 < \psi_1(1 - g_1)$. If $R_0\varphi_2 > 1$ then the condition $\varphi_2 > \varphi_1$ is sufficient as well as necessary for the invasion of strategy 2 at sufficiently high carrying capacity, but if not we also require the stronger condition that strategy 2 have a higher maximum attainable parasitism pressure than strategy 1,

$$\pi_2^* = \frac{R_0\theta_2 - 1}{R_0(\theta_2 - \varphi_2)} > \frac{R_0\theta_1 - 1}{R_0(\theta_1 - \varphi_1)} = \pi_1^*. \tag{21}$$

This is satisfied if $R_0\theta_2 - 1$ is sufficiently high and $\theta_2 - \varphi_2$ is sufficiently small, i.e. ψ_2 sufficiently close to 1 and g_2 sufficiently low.

5.4. Two concurrent defence mechanisms

Let θ_3 and φ_3 be the pay-off factors for the combined strategy in the absence of and in the presence of parasitism, respectively. For a simple multiplicative model for fitness in the absence of parasitism, we would have

$$\theta_3 = \theta_1\theta_2.$$

Other models are possible, but in general we expect that $\theta_3 < \theta_1$ and $\theta_3 < \theta_2$.

We need to derive a formula for φ_3, or equivalently for the expected number of offspring of a parasitised host of type 3. We shall assume that such a host employs

strategies 1 and 2 concurrently with independent outcomes. Let the expected number of offspring per year conditional on successful defence be given by $R\theta_3\psi_3$, with $\psi_3 < 1$. For a multiplicative model, we would have $\psi_3 = \psi_1\psi_2$. We shall see that this is not appropriate for our particular brood-parasite systems, but in general we expect $\psi_3 < \psi_1$ and $\psi_3 < \psi_2$. Since strategies 1 and 2 lead to successful defence with probabilities $1 - g_1$ and $1 - g_2$, and strategy 3 is successful if either 1 or 2 is, the assumption of independence implies that the probability of successful defence with strategy 3 is $1 - g_3$, where $g_3 = g_1g_2$. Hence,

$$\varphi_3 = \theta_3\psi_3(1 - g_1g_2). \tag{22}$$

Let us consider the particular case that strategy 2 is unconditionally blocked by strategy 1, $\theta_2 < \theta_1$ and $\varphi_2 < \varphi_1$. Is it nevertheless advantageous to use strategy 3, strategy 2 *in addition* to strategy 1, if the parasitism pressure is sufficiently high? Strategy 1 is fitter than strategy 3 in the absence of parasitism, since $\theta_3 < \theta_1$, so a necessary condition for strategy 3 ever to prevail is that strategy 3 must be fitter at high parasitism pressure, $\varphi_3 > \varphi_1$, which reduces to

$$\theta_3\psi_3(1 - g_1g_2) > \theta_1\psi_1(1 - g_1). \tag{23}$$

The interpretation of this is that the probability of success of strategy 3, multiplied by the pay-off factors inherent in using it, must outweigh the success of strategy 1, multiplied by its pay-off factors, so that g_2 cannot be too large and θ_3 and ψ_3 cannot be too small compared to θ_1 and ψ_1. In particular, a strategy with $g_2 = 0$ can offer a Pyrrhic victory, and will not be advantageous if θ_3 and ψ_3 are too small.

Even if this inequality holds, we still require the additional condition that strategy 3 have a higher maximum attainable parasitism pressure than strategy 1,

$$\pi_3^* = \frac{R_0\theta_3 - 1}{R_0(\theta_3 - \varphi_3)} > \frac{R_0\theta_1 - 1}{R_0(\theta_1 - \varphi_1)} = \pi_1^*, \tag{24}$$

for strategy 3 to be advantageous in an environment with a sufficiently high host carrying capacity; we see in addition to the conditions above that $R_0\theta_3 - 1$ must not be too small and $\theta_3 - \varphi_3$ must not be too large.

5.5. Two consecutive defence mechanisms

On the other hand, if the defence mechanisms are employed consecutively, the pay-off factor of employing strategy 3 is only applied if (i) the host is parasitised and (ii) strategy 1 is unsuccessful. However, if delay is costly, this factor may be $\psi_3' < \psi_3$, less than it would have been without the delay. Again assuming independent outcomes for the defence strategies, we have

$$\varphi_3 = \theta_3(\psi_1(1 - g_1) + \psi_3' g_1(1 - g_2)). \tag{25}$$

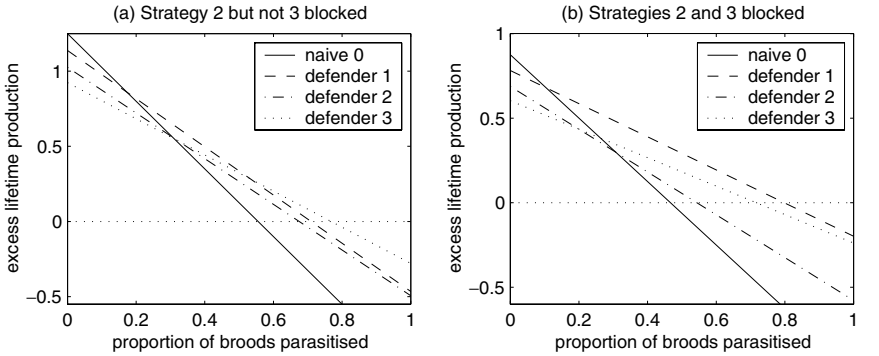

Fig. 4 The particular case that strategy 2 offers certain success, yet is unconditionally blocked by strategy 1. In panel (a) strategy 3 is adaptive for sufficiently high parasitism pressure, while in panel (b) strategy 3 is also unconditionally blocked.

If $\psi_3' = \psi_3$, so that the delay is cost-free, then this is always larger, and strategy 3 is always fitter, than in the concurrent case (22). It always pays to delay strategy 2 in this case, but this is not necessarily true if there are costs associated with the delay. The condition $\varphi_3 > \varphi_1$ reduces to

$$\theta_3\psi_3 g_1(1-g_2) > (\theta_1-\theta_3)\psi_1(1-g_1), \tag{26}$$

where we have dropped the prime on ψ_3. The probability of strategy 2 being successful after strategy 1 has failed, multiplied by the pay-off factor inherent in using strategy 2 in this situation, must outweigh the probability that strategy 1 on its own succeeds, multiplied by the costs saved by not employing strategy 2 in this situation. If this holds, then strategy 3 is advantageous in an environment with a sufficiently high host carrying capacity as long as

$$\pi_3^* = \frac{R_0\theta_3 - 1}{R_0(\theta_3 - \varphi_3)} > \frac{R_0\theta_1 - 1}{R_0(\theta_1 - \varphi_1)} = \pi_1^*, \tag{27}$$

or

$$\frac{R_0\theta_3 - 1}{\theta_3(1-\psi_1(1-g_1)-\psi_3 g_1(1-g_2))} > \frac{R_0\theta_1 - 1}{\theta_1(1-\psi_1(1-g_1))}. \tag{28}$$

This inequality holds if $\theta_2 = 1$, so that it is always worth keeping a strategy in reserve if it does not cost to do so. Otherwise, it fails to hold if $R_0\theta_3 - 1$ is too small, if θ_3 or ψ_3 is too small compared to θ_1 or ψ_1, or if g_2 is too large.

6. Two brood-parasite systems

When a brood parasite lays an egg in the nest of its host, the host may in theory attempt to defend itself by rejecting the egg (strategy 1), or by rejecting the chick

(strategy 2), or by trying both of these consecutively (strategy 3). We shall estimate the relevant parameters for two such systems where different defence strategies are observed.

6.1. Common cuckoo and reed warbler system

Populations of reed warblers *Acrocephalus scirpaceus* parasitised by the common cuckoo *Cuculus canorus* typically adopt one of two strategies, the naive strategy (0) or the egg-rejector strategy (1). The chick-rejector strategy is not usually adopted, either in combination with egg-rejection (3) or alone (2), although there has been a report of chick rejection by desertion (Grim et al., 2003). Egg rejectors are prone to recognition errors; Davies (2000, p. 67) estimates the probability that an unparasitised egg-rejecting reed warbler rejects one or more of its own eggs, a type-I or false-positive error, at 0.3 per brood, and the average number lost in this case as 1.2 eggs, so the expected loss per brood is 0.36 eggs. Since reed warblers normally raise a single clutch of about four chicks in a year, we estimate θ_1, the pay-off for this strategy in the absence of parasitism compared to that for the naive strategy $\theta_0 = 1$, as

$$\theta_1 = 1 - 0.36/4 = 0.91,$$

to two significant figures. There are no data on chick-rejection errors, of course, since reed warblers do not reject chicks. We shall assume that, if they did, the probability of a type-I error would be similar to that for eggs, so that

$$\theta_2 = 0.91.$$

The pay-off for the all-rejection strategy 3 depends on the assumptions made about the probability of making false-positive errors at both stages and the pay-off in this case, but this is a rare event and the details are not important. As a working assumption, we take a multiplicative fitness model,

$$\theta_3 = \theta_1\theta_2 = 0.83,$$

to two significant figures.

Now, consider the pay-offs to parasitised reed warblers. The naive strategy has $\varphi_0 = 0$. Davies (2000, p. 66) estimates the probability that an egg-rejecting reed warbler will recognise and eject a cuckoo egg in its nest as 0.7, so that

$$g_1 = 0.3.$$

We assume chick rejection would have a similar failure rate,

$$g_2 = 0.3.$$

When the cuckoo parasitises the nest it removes one (or sometimes more) of the reed warbler eggs; again assuming a typical clutch size of four, this represents a cost of at least 25% paid by all parasitised hosts. In addition, in rejecting a cuckoo egg

the host may damage one of its own eggs, or it may reject one of them in addition to the cuckoo egg. Davies (2000, p. 66) estimates this extra cost as 0.5 eggs, so that

$$\psi_1 = 0.63.$$

The chick-rejection strategy also involves additional costs. When the cuckoo chick hatches out, it sets about ejecting the reed warbler eggs and/or chicks from the nest. Unless the reed warbler identifies it immediately, it will cause some damage. It is difficult to estimate how much, but we must certainly have $\psi_2 < 0.75$. We shall take

$$\psi_2 = 0.5.$$

Hence, we have

$$\varphi_1 = \theta_1\psi_1(1 - g_1) = 0.50, \quad \varphi_2 = \theta_2\psi_2(1 - g_2) = 0.34.$$

The factor ψ_2 (and not $\psi_1\psi_2$) is also the pay-off factor for the all-rejector that fails to identify a cuckoo egg, so that the pay-offs are not multiplicative. Equation (25) then gives

$$\varphi_3 = 0.58.$$

Annual mortality rates for reed warblers are between about 49 and 63% (Cramp, 1988; Cramp and Brooks, 1992), and we shall take the mean of these, $\nu = 0.56$. The annual basic reproductive ratio is more difficult to estimate. For population survival, we must have $R > \nu$, and we shall take $R = 0.8$, so that the lifetime basic reproductive ratio is

$$R_0 = 1.4.$$

We shall discuss the effect of varying this later. Fortunately, it does not affect the values π_{ij} that determine the crossing points, only the maximum attainable parasitism pressures π_i^*.

6.2. Horsfield's bronze-cuckoo and superb fairy-wren system

Superb fairy-wrens *Malurus cyaneus* have a complex egg-rejection strategy as a defence against brood parasitism by Horsfield's bronze-cuckoos *Chrysococcyx basalis* (Langmore et al., 2003). In particular, they very successfully reject (i) cuckoo eggs that are laid before they have started laying, by sewing the egg into the lining of their nest (13 out of 15 cases recorded in Langmore et al. (2003)), and (ii) cuckoo eggs that are laid after they have finished laying, by deserting the nest (7 out of 8 cases in Langmore et al. (2003)). They very rarely reject cuckoo eggs that are laid during their laying period (1 out of 53 cases in Langmore et al. (2003)). Unless the cuckoo gives the game away by laying at the wrong time, the hosts are (almost always) egg-acceptors. The cuckoo eggs are indeed mimetic, white and finely speckled, but experiments have shown that the hosts will not reject model

eggs even if they are blue with large polka dots (Brooker and Brooker, 1989). However, they do seem to employ a chick-rejection strategy (Langmore et al., 2003). A Horsfield's bronze-cuckoo chick exhibits similar behaviour to a common cuckoo chick, ejecting host eggs and/or chicks in the nest and becoming its sole occupant. The superb fairy-wren's strategy is sometimes to desert a nest containing a single occupant. The probability that they do this is about 0.4 when the occupant is a cuckoo, so that $g_2 = 0.6$, and about 0.26 when it is a fairy-wren. Why has this strategy, which seems so error-prone, evolved? Let us compare pay-offs for the egg-rejection (1) and chick-rejection (2) strategies as defences against cuckoos that lay during the host laying period. Assuming that superb fairy-wrens are indeed egg-acceptors under these circumstances, we have no data on potential error rates. We shall instead use the chick-rejection data, and take the probability of a false-positive identification as 0.26, and that of failing to identify a cuckoo egg as $g_1 = 0.6$. A typical superb fairy-wren clutch size is three eggs, so

$$\theta_1 = 1 - 0.26/3 = 0.91,$$

to two significant figures. Just as the common cuckoo does, the Horsfield's bronze-cuckoo removes a host egg when it parasitises a nest, so that

$$\psi_1 = 1 - 1/3 = 0.67$$

and

$$\varphi_1 = \theta_1 \psi_1 (1 - g_1) = 0.24,$$

both to two significant figures. The cost of strategy 2 in the absence of parasitism is the loss of the brood in 26% of cases when that brood consists of a single chick. However, this only occurs in 4% of broods, so the expected loss cannot exceed 1%. We shall take

$$\theta_2 = 0.99.$$

The penalty for successfully employing the strategy is loss of the brood. However, Brooker and Brooker (1998) argue that this penalty is less severe than it might seem. Fairy-wrens tend to limit the number of young they raise in a season, to avoid local over-crowding. The breeding season is long (20 weeks), and it is quite possible for a pair of parasitised fairy-wrens to make up for lost time and raise the same number of young as an unparasitised pair. This is especially true because a bronze-cuckoo chick takes less time and resources to raise than a brood of fairy-wrens. (In contrast, the reed warbler breeding season is short (10 weeks), and a common cuckoo chick takes more time to raise than a brood of reed warblers.) Let us take

$$\psi_2 = 0.5,$$

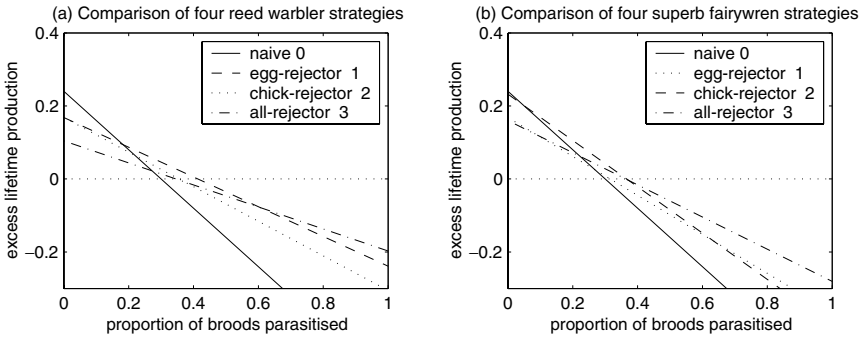

Fig. 5 The excess fitness functions v_0, v_1, v_2 and v_3 for cuckoo hosts. Panel (a) represents the common cuckoo and reed warbler system, and panel (b) the Horsfield's bronze-cuckoo and superb fairy-wren system. It can be seen that types 2 and 3 never make an appearance in (a), while types 1 and 3 never make an appearance in (b). In both cases, the all-rejection strategy would be fittest if the parasitism pressure could attain sufficiently high values, which might occur for sufficiently high values of k and R_0. For a sketch of the corresponding (k, R_0) plane, see Fig. 6(a), with say $R_0 = 1.4$.

and

$$\varphi_2 = \theta_2\psi_2(1 - g_2) = 0.20.$$

The pay-off for strategy 3 in the absence of parasitism is $\theta_3 = \theta_1\theta_2$. With parasitism, it is

$$\varphi_3 = \theta_1\theta_2(\psi_1(1 - g_1) + \psi_2 g_1(1 - g_2)), \tag{29}$$

as in the reed warbler case. Numerically,

$$\theta_3 = 0.9, \quad \varphi_3 = 0.35.$$

We shall take the same values for R and ν as for reed warblers, $R = 0.8$, $\nu = 0.56$, so that we again have

$$R_0 = 1.4.$$

7. Results

The graphs of excess production v_i of host type i against parasitism pressure π, for $i = 0$, 1, 2 and 3, are shown for both systems in Fig. 5. We can immediately read off from these figures the possible behaviours of the systems for different parasitism pressures π. Consider the common cuckoo and reed warbler system, panel (a). For π low the naive host type will prevail. As π increases, a mutant egg-rejecting host type would invade and go to fixation, beyond $\pi = \pi_{01}$. If it were

possible for π to increase towards 1, then a mutant all-rejecting type would invade and go to fixation, beyond $\pi = \pi_{13}$. However, this cannot happen. Instead the line of zero excess production $v = 0$ is approached, at $\pi = \pi_1^*$, and the hosts continue to use a single (egg-rejecting) defence strategy. Neither chick-rejectors nor all-rejectors ever invade. On the other hand, if egg-rejection never evolved for some reason, a mutant chick-rejector would invade the naive type and go to fixation beyond $\pi = \pi_{02}$. Chick-rejection is advantageous in the absence of egg-rejection, but the strategy is blocked by the use of egg-rejection. The Horsfield's bronze-cuckoo and superb fairy-wren system, panel (b), behaves similarly, but with the roles of egg-rejection and chick-rejection reversed; in this case, the egg-rejection strategy is blocked by chick-rejection. The ecology of these systems is crucial to the results, since the strategy-blocking is conditional on the ecological parameters.

Comparisons of parameter values between these systems show quite substantial differences. The φ values in the first system are substantially greater than those in the second, essentially because superb fairy-wrens are worse at recognising the parasite chick than reed warblers are at recognising the parasite egg. In both cases $\varphi_1 > \varphi_2$, so that egg rejection would be better than chick rejection in the hypothetical case of certain parasitism, simply because of the delay and damage that chick rejection entails. However, the difference that is crucial in determining which strategy is blocked is in θ_2, the relative pay-off of chick rejection in the absence of parasitism, when costs are a result of a false-positive identification of the host's chick as a parasite's. The reed warbler pays a heavy price.

8. Discussion

8.1. Competitive exclusion of types

As a consequence of competition between types, under our assumptions of ecologically identical hosts, only one type will persist unless the parasitism pressure takes one of a few special values π_{ij}. However, a bifurcation analysis shows that in many cases the parasitism pressure does indeed take one of these values for all values of the bifurcation parameter k in non-trivial intervals $[k_{ij}, k_{ji}]$ with $k_{ij} < k_{ji}$. Figure 6 shows that populations with mixed strategies do exist in some regions of parameter space. They are an important feature of host–parasite systems with more than one host type, although it happens that for typical values of the ecological parameters they are not seen in either of our host–cuckoo systems.

8.2. Pyrrhic victories and strategy-blocking

We have seen three kinds of Pyrrhic victory, where strategies that offer certain success in defeating the parasite are nevertheless not advantageous, the first in Section 5.2, the second in Section 5.3, and the third in Section 5.4. In Section 5.2, the reason that the defence strategy is disadvantageous is that the ecological parameters restrict host and therefore parasite populations, and that therefore the rare-enemy effect comes into play. More explicitly, defence strategy 1 is only

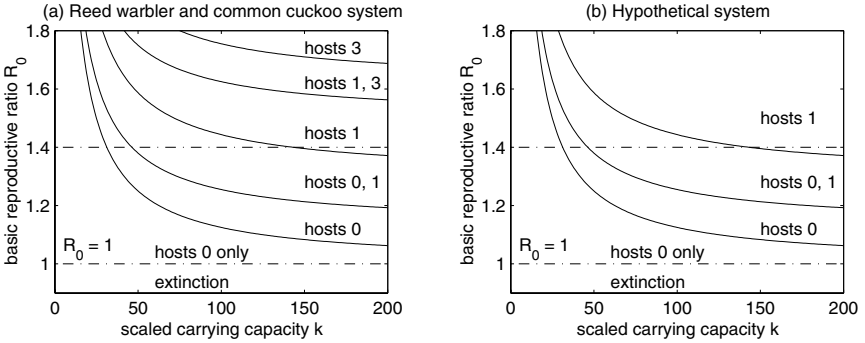

Fig. 6 (a) A diagrammatic representation of the surviving host types in the common cuckoo and reed warbler system as a function of the ecological parameters R_0 and k. For $R_0 < 1$, both hosts and parasites go extinct. In the region labelled "hosts 0 only," parasites go extinct and only naive hosts survive. In the rest of the diagram, both hosts and parasites survive, and the diagram shows the surviving host types. The bifurcation diagram, Fig. 1(b), took $R_0 = 1.4$, and the bifurcation points there can also be read off from the line $R_0 = 1.4$ shown here. Strategy 2 (on its own or in combination with 1) is blocked for all k at $R_0 = 1.4$. However, it can be seen that if both R_0 and k were sufficiently high then we would see hosts with the combined strategy 3 appearing, so that the blocking is conditional on the ecological parameters. (b) A similar diagram for a hypothetical system with $\varphi_3 < \varphi_1$. In this case, hosts of type 3 never appear, whatever the values of R_0 and k, and strategy 2 (on its own or in combination with 1) is unconditionally blocked.

advantageous if the parasitism pressure π exceeds a *rarity threshold* π_{01}, and the ecological parameters ensure that this cannot happen. This effect disappears if both k and R_0 are large (see Fig. 2(b) or Fig. 6(b)). In Section 5.3, defence strategy 2 was unconditionally blocked by defence strategy 1 simply because it was too costly, despite its defensive success. In Section 5.4, strategy 2 was again too costly to compete on its own with strategy 1, so it is clear that it will not appear alone as a defence strategy. However, for high parasitism pressure it was fitter than the naive strategy 0, and so it seems that in these circumstances it is better to use strategy 2 than not to use it. Why, then, is it not advantageous to use the combined strategy 3 at high parasitism pressure? Defence strategy 2 alone is fitter than the naive strategy 0 if the parasitism pressure π exceeds a rarity threshold π_{02}. A decision to use strategy 3, i.e. strategy 2 in addition to strategy 1, is in effect a decision to defend against *potential* parasitism pressure of at most g_1. If $g_1 < \pi_{02}$, it is better to refrain from defence strategy 2, because of the rare-enemy effect *extended to apply to the enemies that overcome defence strategy 1*. Strategy 3 is unconditionally blocked by strategy 1. Note that the relative timing of the defence strategies is not important: in the reed warbler and common cuckoo example it is the cuckoo chick that is rare, but in the fairy-wren and bronze-cuckoo example the rare enemy is the bronze-cuckoo egg *that is destined not to be rejected at the chick stage*.

More generally, strategy 3 may be blocked by strategy 1 conditionally on the parasitism pressure (or the ecological parameters), but the explanation is again in terms of an extended rare-enemy effect. For given strategy parameters θ_i, g_i and ψ_i, the strategy-blocking in the two brood-parasite systems depends on the values of the ecological parameters R_0 and k. Figure 6 is a diagram of the regions in

ecological parameter space where each outcome occurs (a) for the common cuckoo and reed warbler system and (b) for a hypothetical system with similar features except that $\varphi_3 < \varphi_1$. In case (a), we see that if R_0 and k were sufficiently large, then the all-rejector strategy would invade, so that here the strategy-blocking is conditional on the ecological parameters. The Horsfield's bronze-cuckoo and superb fairy-wren system is similar, except that strategy 2 replaces strategy 1. In neither of these systems would we expect to see both defence strategies employed under normal circumstances, but might see them if R_0 and k are exceptionally high. In case (b), the strategy-blocking is unconditional: however high R_0 and k, we would never expect to see both defence strategies employed.

8.3. Attack success probabilities and the effects of exploiter coevolution

Let us assume that at some point in evolutionary time a defence strategy 2, either on its own or combined in strategy 3, is blocked by a fixed defence strategy 1. Let us further assume that as evolutionary time passes the exploiter adapts to defence strategy 1, so that its attack success probability g_1 increases, i.e. the defence strategy 1 becomes less successful. Will this process always result in the eventual unblocking of strategy 2? We shall look at the potential invasion of the combined strategy 3; the potential invasion of the single strategy 2 is similar but simpler. Let us first neglect ecological factors, and ask whether the (k, R_0) plane, assumed to look initially like Fig. 6(b), will always come to look like Fig. 6(a), so that strategy 3 can invade for large enough k and R_0. It does so if φ_1, which initially satisfies $\varphi_1 > \varphi_3$, always decreases sufficiently that the opposite inequality is satisfied. Looked at in a different way, we are interested in whether the curve $\varphi_1 = \varphi_3$ is crossed as the attack success probability g_1 increases. A sketch of the curve $\varphi_1 = \varphi_3$ is shown in Fig. 7. It always passes through the points $(1 - \frac{\theta_3\psi_3}{\theta_1\psi_1}, 0)$ and $(1, 1)$ in the (g_2, g_1) plane. For any fixed value of g_2, and any initial value of g_1, an increase in g_1 towards 1 eventually results in the curve being crossed and strategy 2 being unblocked. We have not taken account of any constraints that might limit the maximum value of g_1, and that might therefore prevent this from happening. Such constraints could ensure that strategy 2 is permanently blocked. Let us now consider the effect of ecological factors. For simplicity, we neglect intra-specific competition and focus on the effect of varying R_0, although the effect of varying k is similar. Then, for potential invasion of strategy 3, we need not only $\varphi_3 > \varphi_1$ but also $\pi_3^* > \pi_1^*$. The (g_2, g_1) plane is sketched in Fig. 7 in the two cases $R_0\theta_3\psi_3 < 1$ and $R_0\theta_3\psi_3 > 1$. In either case, there is a critical value of $\hat{g}_2$ of g_2 such that if $g_2 < \hat{g}_2$ then strategy 2 is eventually unblocked (left arrows in Fig. 7), whereas if $g_2 > \hat{g}_2$ then it remains blocked (right arrows in Fig. 7). For given costs, i.e. given pay-off factors θ_3 and ψ_3, then strategy 3 will eventually invade as long as the defence success probability $1 - g_2$ is sufficiently high, but not otherwise.

We have focussed in this section on the effect of the defence success probability, but similar results hold if we focus on the other parameters. For example, if θ_3 and g_2 are fixed, and g_1 again increases to 1, strategy 3 eventually invades as long as ψ_3 is sufficiently high.

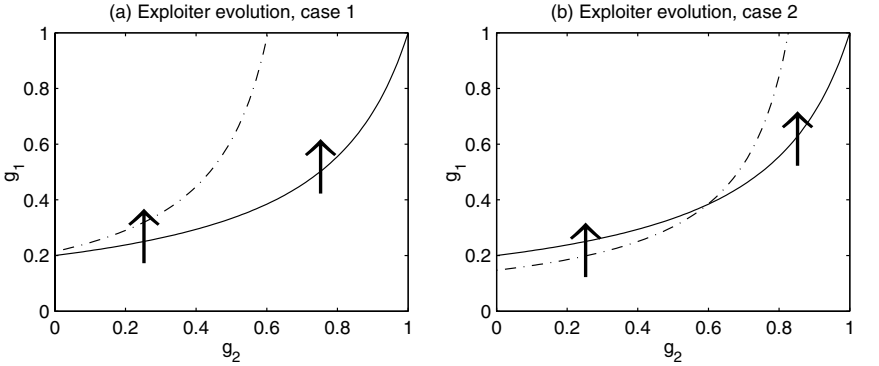

Fig. 7 Diagrams showing the effect of exploiter evolution, (a) for $R_0\theta_3\psi_3 < 1$ and (b) for $R_0\theta_3\psi_3 > 1$. The solid lines are the curves $\varphi_1 = \varphi_3$, and the dash-dotted lines the curves $\pi_1^* = \pi_3^*$. The arrows represent evolutionary trajectories, where the exploiter is evolving to reduce the success probability $1 - g_1$ of the defence strategy 1, i.e. to increase g_1. All arrows begin in the region where both $\varphi_1 > \varphi_3$ and $\pi_1^* > \pi_3^*$, so that strategy 3 is unconditionally blocked. In (a), the arrows both cross $\varphi_1 = \varphi_3$ into the region where strategy-blocking is conditional on the ecological parameters; the right arrow remains there permanently, while the left arrow enters the region where strategy 3 is unblocked. In (b), the right arrow represents similar behaviour to the right arrow in (a), while the left arrow moves directly from the unconditionally blocked region to the unblocked region on crossing the solid line: here, crossing the dash-dotted line has no effect on the behaviour. In both panels, the left arrow represents a value $g_2 < \hat{g}_2$, and the right arrow a value $g_2 > \hat{g}_2$.

8.4. Other exploiter–victim systems

We have restricted our attention to brood-parasites and their hosts, but the same general conclusions should emerge from other exploiter–victim systems. In particular, the results carry over immediately to host–parasitoid systems, which can be modelled as a particular case of our system. Simlar results may be obtained in predator–prey systems modelled using differential equations (Section A.3). We have restricted attention to systems that have stable steady-state solutions. We expect similar principles to emerge in oscillatory systems, but the analysis then presents more of a challenge.

8.5. Strategy-blocking over three trophic levels

The ideas in this paper give new insight into the interaction between defence strategies and the working of the rare-enemy effect. They may also explain paradoxes in other parasitic systems. For example, when there is more than one level of parasitism, we can now understand why some species fail to recognise their own friends. Ant colonies of the species *Myrmica* are sometimes parasitised by Mountain Alcon Blue butterfly larvae *Maculinea rebeli* (Akino et al., 1999). Ants generally defend themselves against parasitism by recognising and rejecting foreign organisms in their nests, but the butterfly counters this defence by mimicking the ant recognition pheromones, so closely that the caterpillar is carried by the ants into their nest. The nest may then be invaded and the caterpillar parasitised by *Ichneumon eumerus* wasps. A chemical cocktail that provokes in-fighting among

the ant workers (Thomas et al., 2002) allows the wasp to gain access to and lay its egg in the caterpillar. Although the wasps help relieve the ants from their parasites, the ants clearly do not recognise them as their allies: they do not pursue any active strategy to attract them, or even the passive strategy of allowing them free access to their nest. Such strategies could involve costly recognition errors, and we suggest that the beneficial wasp is simply too rare to be recognised as a friend. The wasp is rare because the butterfly is rare: the extreme specialisation within this system drives a *rare-friend effect*.

Plant defensive strategies against insect herbivores often involve those herbivores' natural enemies (Price et al., 1980; Sabelis et al., 2002). We have discussed an example in the mutualistic relationship between swollen-thorn acacias and acacia ants (Janzen, 1966). Acacias employ either this defence strategy or chemical defences against herbivores, not both, so it seems that in this case either strategy may block the other. As an example where strategy-blocking does not occur, caterpillar-damaged plants may protect themselves by emitting chemicals that attract parasitic wasps (Turlings et al., 1995). The primary role of the chemicals is probably as toxic deterrents against the herbivore, but it does seem that they have evolved as signals and not merely cues. In this case, the cost to the plant of producing chemicals that are effective signals as well as effective toxins is clearly outweighed by the benefits. We have not found data on caterpillar infestation rates in such situations, but we would predict that either the production cost is low, or infestation rates are so high that the plant's friend is not rare.

9. Conclusions

We expect to see strategy-blocking very generally in exploiter–victim systems, on two or more trophic levels, although it may disappear as the exploiter evolves counter-measures to the victim's defence. It occurs when victims employing one defence strategy (strategy 1) are fitter than those employing another, either as a replacement for (strategy 2) or in addition to (strategy 3) the first. It is paradoxical because strategy 2 alone would be advantageous against naive hosts (strategy 0), at least when parasitism pressure is high, so it seems that the combined strategy 3 must be fitter than strategy 1 alone. Strategy 1 renders the addition of strategy 2 disadvantageous, as a consequence of the rare-enemy effect (Dawkins, 1982) extended to the *potential* enemies that would survive strategy 1 alone. Strategy-blocking may be conditional on the ecological parameters, in which case we would expect to see the combined strategy employed if both the host carrying capacity and the basic reproductive ratio were sufficiently high, or it may be unconditional, whatever the ecological parameters. It is therefore essential to consider the ecology of the system in any discussion of the evolutionary basis of defence portfolios, and failure to do so may impair understanding. Generally, we would expect less strategy-blocking, and hence richer defence portfolios, in richer environments; this tendency is illustrated in Fig. 6(a) and an example in the field is the increase in plant toxins with butterfly density (Levin, 1976). We suggest that strategy-blocking conditional on the ecological parameters is the reason that we

do not observe chick-rejection in many brood-parasite systems, and why, when we do, we do not observe egg-rejection.

Appendix

A.1 Conditions on the self-limitation function Ψ

The analysis can be carried through for a general model of contest competition, i.e. for a function Ψ of H and a parameter $k \in (0, \infty)$ satisfying $\Psi(0;k) = 1$, $\Psi(H;k) \to 0$ as $H \to \infty$,

$$\Psi'(H;k) < 0, \quad \frac{\partial}{\partial H}(H\Psi(H;k)) = H\Psi'(H;k) + \Psi(H;k) > 0, \tag{A.1}$$

where a prime denotes differentiation with respect to H. The parameter k is related to the host carrying capacity, and we shall assume $\Psi(H;k) \to 0$ as $k \to 0$, $\Psi(H;k) \to 1$ as $k \to \infty$, and

$$\frac{\partial \Psi}{\partial k}(H;k) > 0. \tag{A.2}$$

A.2 Monotonicity of P_i^* *and* H_i^*

From Eqs. (11) and (12),

$$(\mu + cgf'(P)H)\frac{\partial P}{\partial k} - cg(1 - f(P))\frac{\partial H}{\partial k} = 0, \tag{A.3}$$

$$w'(P)\frac{\partial P}{\partial k} + \frac{\Psi'(H)}{(\Psi(H))^2}\frac{\partial H}{\partial k} = -\frac{1}{(\Psi(H))^2}\frac{\partial \Psi}{\partial k}. \tag{A.4}$$

Hence $\frac{\partial P}{\partial k} = \Delta_1/\Delta_0$, $\frac{\partial H}{\partial k} = \Delta_2/\Delta_0$, where

$$\Delta_0 = \begin{vmatrix} \mu + cgf'(P)H & -cg(1 - f(P)) \\ w'(P) & \Psi'(H)/(\Psi(H))^2 \end{vmatrix},$$

and so on. On curve (11), and in particular at (P_i^*, H_i^*),

$$\Delta_0 = \frac{\mu}{1 - f(P)}(1 - f(P) + Pf'(P))\frac{\Psi'(H)}{(\Psi(H))^2} + cg(1 - f(P))w'(P) < 0,$$

using (8). It is easy to show that $\Delta_2 < 0$ on curve (11), and that $\Delta_1 < 0$ everywhere in the positive quadrant, so that P_i^* and H_i^* are increasing functions of k.

A.3 Models in continuous time

In continuous time, an analogous model for a parasite and two hosts is given by

$$\frac{\mathrm{d}P}{\mathrm{d}t} = cg_i(1 - f(P))H_i + cg_j(1 - f(P))H_j - \mu P, \tag{A.5}$$
$$\frac{\mathrm{d}H_i}{\mathrm{d}t} = H_i\left(w_i(P) - \frac{H}{k}\right), \quad \frac{\mathrm{d}H_j}{\mathrm{d}t} = H_j\left(w_j(P) - \frac{H}{k}\right),$$

where the net *per capita* growth rate w_i of H_i in the absence of competition is given by

$$w_i(P) = r\theta_i f(P) - r(\theta_i - \phi_i)(1 - f(P)) - \nu. \tag{A.6}$$

The parameters have analogous meanings to those in the discrete-time model. The host competition term is logistic, with $H = H_i + H_j$, and k is a scaled host carrying capacity in the absence of parasitism. In the absence of competition and parasitism the *per capita* birth rate of H_i is given by $r\theta_i$, which is reduced to $r\phi_i$ in parasitised hosts.

In the absence of parasitism, $\mathrm{d}/\mathrm{d}t(H_i/H_j) = r(\theta_i - \theta_j)(H_i/H_j)$, and each H_i is bounded, so that all host types tend to extinction except the one with the largest value of θ_i, (as in the discrete-time case the one following the naive strategy), which satisfies $H_i(t) \to H_i^0 = k(r\theta_i - \nu)$. The bifurcation analysis as the parameter k increases now proceeds exactly as in the discrete-time case. As $k \to \infty$, the last remaining host type is the one with the highest value of $(r\theta_i - \nu)/(r(\theta_i - \phi_i))$.

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